CLAUSEN AND UHL: SEDUM

THE TAXONOMY AND CYTOLOGY OF THE SUBGENUS GORMANIA OF SEDUM

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INTRODUCTION

The species of Sedum comprising the subgenus Gormania seem to constitute a natural group in biological relationship. In geographical distribution, they are all restricted to the Pacific Mountain System of Western North America. Some of the principal points of this discussion appeared in a brief abstract in the American Journal of Botany (4). The detailed evidence for the statements made there are herein presented.

Historically, the species which we assign to the subgenus Gormania have had a troubled nomenclatural career. They have been referred variously to Cotyledon, Echeveria, Gormania and Sedum. The senior author (3) has already given his reasons for regarding this group of species as a subgenus of Sedum. Continued study and additional evidence have not altered this point of view. Sedum spathulifolium clearly belongs to the Gormania series, yet it is too close to typical Sedum to warrant generic segregation. Characters seem lacking by which it might be segregated from Sedum on a generic basis. Our data clearly indicate the alignment of S. spathulifolium with the true Gormaniae, yet it has petals distinct to the base, a detail also emphasized by Britton and Rose (2). S. spathulifolium affords a direct living connection between typical Sedum and the extreme types of section Eugormania. The separate petals of S. spathulifolium and the closely related S. Purdyi, usually regarded as an indication of morphological primitiveness, seem to strengthen the idea that these two species are less advanced phylogenetically than the other species of Gormania. They may be regarded as constituting a separate section from which Eugormania probably has evolved. It is interesting to note that S. spathulifolium, supposedly the most primitive species in the subgenus, is the most widely distributed; also, the other species all occur within its distributional area.

Three authors have rather recently accounted for the species which we place in subgenus Gormania. A comparison is interesting to show the differences in interpretation. Praeger (12), though considering only cultivated species, treated four of the binomials which we refer to subgenus Gormania. He assigned all of these to the section "Seda Genuina," group Spathulifolia, in which he also placed two other species. The six binomials, our disposition of them when we do not regard them as valid species, and the chromosome number for each, follow:

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S. spathulifolium Hooker — n = 15, 2n = 30

- S. yosemitense Britton = a subspecies of S. spathulifolium n = 15
- S. rubroglaucum Praeger = S. obtusatum subsp. typicum
- S. Hallii (Britton) Praeger = S. obtusatum subsp. typicum 2n = 30
- S. oreganum Nuttall n = 12
- S. divergens S. Watson -2n = ?16

Berger (1) referred the species of Gormania, along with others, to two different groups of section "Seda Genuina." Below are listed all the species which he included in these groups, with those starred which we place in the subgenus Gormania.

- Group 5. Americana
 - S. longipes Rose
 - S. filiferum S. Watson
 - S. Lumholtzii Robinson & Fernald
 - S. puberulum S. Watson = S. Griffithsii Rose
 - S. Wootonii Britton = S. Cockerellii Britton n = 16
 - S. Griffithsii Rose n = 14, 29
 - S. Wrightii A. Gray n = 12, 36
 - S. Nevii A. Gray n = 6
 - S. Nevii A. Gray var. Beyrichianum (Masters) Praeger = S. Beyrichianum Masters — n = 14, 28
 - S. madrense S. Watson
 - *S. californicum Britton = S. spathulifolium Hook.
 - S. bellum Rose
 - S. versadense Thompson
 - *S. Burnhamii (Britton) Berger = S. obtusatum Gray subsp. typicum - 2n = 30
 - *S. laxum (Britton) Berger = S. laxum subsp. typicum -2n = 30
 - *S. sanhedrinum Berger = S. laxum subsp. retusum
 - *S. Eastwoodiae (Britton) Berger = S. laxum subsp. retusum -2n = 30
- Group 23. Rosulata
 - *S. spathulifolium Hooker n = 15, 2n = 30
 - *S. pruinosum Britton = a subspecies of S. spathulifolium n = 15, 2n = 30
 - *S. yosemitense Britton = a subspecies of S. spathulifolium n = 15
 - S. Leibergii Britton
 - *S. Woodii Britton = typical S. spathulifolium n = 15
 - *S. Watsonii (Britton) Berger = S. oregonense (Watson) Peck - 2n = 90
 - *S. obtusatum A. Gray = S. obtusatum subsp. typicum 2n = 30

S. debile S. Watson — 2n = 14-18S. oreganum Nutt. — n = 12

The various chromosome numbers which appear in the above lists are explained and discussed in a recent article in Brittonia (5).

Fröderström (8) recognized Gormania as a separate genus, including in it G. obtusata, G. Watsoni, G. anomala and G. rubroglauca. He placed in two different groups of Sedum, under "Americana Kyphocarpia," other of the names which we refer to Gormania. These are starred in the following lists.

Group Ternatum

 \bar{S} . ternatum Michx. — 2n = 16, 24, 32, 48

S. Nevii A. Gray — n = 6

- *S. californicum Britton = a subspecies of S. spathulifolium S. bellum Rose
- Group Spathulifolium
 - *S. spathulifolium Hooker $n = 15^{\circ}$
 - *S. pruinosum Britton = a subspecies of S. spathulifolium n = 15
 - S. Leibergii Britton
 - *S. Woodii Britton = typical S. spathulifolium n = 15
 - *S. yosemitense Britton = a subspecies of S. spathulifolium n = 15

Our own arrangement follows:

Section 1. Rosulata

- S. spathulifolium (including S. anomalum, S. californicum, S. pruinosum, S. Woodii and S. yosemitense) n = 15, 2n = 30S. Purdyi — n = 15
- Section 2. Eugormania

S. obtusatum — n = 15, 2n = 30

- S. oregonense 2n = 90
- S. laxum n = 15, 2n = 30
- S. Moranii 2n = 30

Sedum oreganum, for which the senior author (3) created the section Oreganica, clearly does not belong to the Gormania series. In habit, it is at once different, without prominent basal rosettes of leaves. Also, the petals are straight, not erect below and then spreading. Further, the chromosomes, though comparable in size with those of the species of subgenus Gormania, exhibit a greater range in size among the members of the same complement. Also, the haploid number is 12. Probably S. oreganum should be dropped from subgenus Gormania and referred to another subgenus of Sedum. Our data for this species are based on various living plants which originated in the state of Washington. The chromosome counts were made from collections of Professor W. C. Muenscher (7923 and 7929).

In the present work, the taxonomic study is by R. T. Clausen, the cytological investigation by C. H. Uhl. The collecting of plants for this study was made possible by grants from the Penrose Fund of the American Philosophical Society and the Trustee-Faculty Committee on Research of Cornell University. The cytological work was made possible by the grant from the Trustee-Faculty Committee. The plants in cultivation have been grown and maintained through the courtesy of the Department of Floriculture of Cornell University.

METHODS AND MATERIALS

We continue to employ the category of subspecies for the major morphological races of species which are geographically correlated because no really valid argument has yet been advanced against such usage. The criticisms by Fosberg (7) and Weatherby (13) fail to cope with the problem of horticultural Horticulturists continue to designate minor genetical varieties. variations of species, not geographically correlated, as varieties, ignoring the arguments of Fernald, Weatherby and Fosberg, who presumably would designate such variants as forms. For examples of the use of variety by tradesmen and horticulturists, see the 1943 catalog of W. Atlee Burpee Co. (pages 26, 27 et al) or the recent bulletin on grapes by Magoon and Snyder (11). The International Rules of Nomenclature do not outlaw subspecies for the groups which we so designate. On the other hand, a convincing argument can be constructed the other way. Most botanical and horticultural varieties are very minor genetic variations. These variations often are of great economic or horticultural significance, but phylogenetically are not yet important enough to be regarded either as species or subspecies. These should, in our opinion, be designated as varieties. They are numerous, really too numerous to warrant assigning botanical names to each, yet many have been named. Forms are the phenotypic variations of the same genotype. In Sedum they can frequently be produced by giving the plants more water than normal or by placing them in dense shade. They are usually physiological in origin and are best designated merely by descriptive vernacular terms.

The living plants which are the real basis for our classification were obtained for the most part in the summer of 1940 when Mr. Harold Trapido and the senior author collected extensively on the Pacific slope. Details of distribution have been obtained from a study of specimens in various herbaria. In the citations, names of these are abbreviated as: (BH) Bailey Hortorium, Ithaca, New York; (CAS) California Academy of Sciences, San Francisco; (CLOK) Clokey Herbarium at the University of California, Berkeley; (CU) Cornell University, Ithaca, New York; (DS) Dudley Herbarium, Stanford University, California; (FM) Field Museum of Natural History, Chicago Illinois; (NY) New 1944]

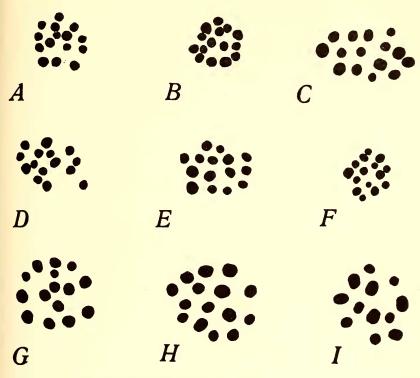


FIG. 1. Chromosome complements. A, Sedum spathulifolium subsp. typicum, from Josephine County, Oregon (C5010); fixed in craf, n=15. B, S. s. subsp. typicum, from Lake County, California (C4925); fixed in craf, n=15. C, S. s. subsp. pruinosum, from south of Crescent City, Del Norte County, California (C4937), n=15. D, S. s. subsp. anomalum, from San Bernardino Mountains, California (C4748), n=15. E, S. s. subsp. anomalum, from Yosemite National Park, California (C4802); second meiotic metaphase, n=15. F, S. Purdyi, from the canyon of Canyon Creek, Siskiyou County, California (C4983); fixed in craf, n=15. G, S. laxum subsp. retusum, from Mendocino County, California (UC28.3), n=15. H, S. laxum subsp. typicum, from Waldo, Oregon (C5018), n=15. I, S. oreganum, from Lummi Island, Whatcom County, Washington (WCM7925), n=12. Unless otherwise noted, all figures are first meiotic metaphases and fixation was in Carnoy's solution. All drawings are × 3320.

York Botanical Garden, New York, New York; (ORE) University of Oregon, Eugene; (POM) Pomona College, Claremont, California; (UC) University of California, Berkeley; (US) United States National Herbarium, Washington, D. C. We wish to thank the curators at each of these institutions for making their specimens available for study.

The counts of chromosomes are from meiotic material. Most of the young flowers were fixed in Carnoy's fluid (6 parts chloroform, 3 parts absolute alcohol, and 1 part acetic acid), smeared, and stained in aceto-carmine. Some were fixed in craf, em-

bedded, sectioned, and stained in crystal violet. All preparations were examined with a Spencer microscope with $95 \times$ fluorite objective, N.A. 1.25. Drawings were made with a camera lucida, all \times 3320. The chromosomes, as well as metaphase plates, of material fixed in craf and stained in crystal violet were consistently smaller than those of material fixed in Carnoy's. This must be remembered in examining the figures. For purposes of comparison, the drawings, with one exception, are all of first meiotic metaphases.

CYTOLOGY

The details regarding chromosome number and morphology are reported under the various species and subspecies. Great similarity prevails throughout the whole subgenus. All species are n = 15, with the exception of S. oregonense, for which a 2nnumber of about 90 has been determined by Hollingshead (9). Comparison of the chromosome complements of eleven collections of S. spathulifolium, one of S. Purdyi, one of S. laxum subsp. typicum and one of S. laxum subsp. retusum indicate that these species can not be distinguished by their chromosomes. The chromosome complements are very similar, indicating close relationship between the two species of the section Rosulata and species of the section Eugormania. Sedum oreganum, with an n number of 12, seems remote from the species of Gormania and, as has already been suggested, should be dropped from this subgenus. Text figure 1 shows the chromosome complements in the various subspecies of S. spathulifolium and in S. Purdyi, S. laxum and S. oreaanum.

Systematic Account

Gormania, as a subgenus, had its beginning in 1942. The key to the sections of the subgenus, in a recent paper by the senior author (3, pp. 28, 29), may now be emended as follows:

Α.	Petals separate to their bases, erect for about
	one-tenth of length, then widely spreading;
	rosettes with the leaves fleshy, but not
	leathery; inflorescence a 3-parted cyme,
	sometimes compound 1. Section Rosulata
AA.	Petals connivent or united for one-fourth or
	more of length, erect below, divergent above;
	rosettes with the leaves thick and leathery;
	inflorescence a paniculate cyme 2. Section Eugormania
	Section Populata (Bargar) Clausan at Uhl stat nov Groun
_	Section Rosulata (Berger) Clausen et Uhl, stat. nov. Group

Rosulata Berger, in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 18a: 457. 1930. Section Rosulata Clausen and Uhl, nomen nudum, Bull. Torrey Bot. Club 69: 27. 1942. Type species: S. spathulifolium Hooker.

Petals separate throughout their length, erect below for about one-tenth their length, then widely spreading; leaves arranged in prominent rosettes borne on creeping stems which give rise to numerous secondary stems, likewise rosette-bearing; plants frequently producing large patches or mats which may spread for many years by vegetative means.

KEY TO THE SPECIES OF SECTION ROSULATA

A. Rosettes loose, not densely compressed; leaves of rosettes loosely spreading, not closely compacted, minutely crenulate and papillose

AA. Rosettes densely compressed with the leaves closely compacted (pressed close together) and prominently papillate on margins 2. Sedum Purdyi

1. SEDUM SPATHULIFOLIUM Hooker

Perennial; sterile stems 1-3 mm. in diameter, 1-8.5 cm. long, white to pink or red, procumbent or creeping; leaves in prominent rosettes, usually spatulate, blunt or slightly emarginate, crenulate on margins, 0.3-3.2 cm. long, 2-14 mm. wide, 1-3 mm. thick, glaucous or pruinose or glabrous and dark- or vellow-green, sometimes suffused with red or bronze; primary stems usually with secondary offsets below rosettes and these sometimes with tertiary offsets; sterile shoots usually naked except for the rosette at the apex, but sometimes leafy throughout with alternate oblongspatulate leaves, 0.5–1.5 cm. long; floral stems erect or decumbent, 5-30 cm. high, 1-4 mm. thick below inflorescence, with the leaves alternate, spatulate, oblong-spatulate, or elliptic-oblong, reduced downwards, 0.6-2.0 cm. long, 3-8 mm. wide; inflorescence a simple or compound three-parted cyme of 12-51 flowers, with a central flower; floral bracts oblong-spatulate, 4–11 mm. long; flowers sessile or short-stalked on pedicels 1-4 mm. long, usually 5-merous, 0.7-1.7 cm. in diameter; sepals lanceolate or ovate-lanceolate, connate below, 2-4 mm. long; petals lanceolate, acute, concave, 5-8 mm. long, erect below for 2-3 mm., then widely spreading, canary-yellow, rarely orange or white; stamens 4-5 mm. long, yellow; nectar scales 0.5 mm. long, 0.2 mm. wide, transversely oblong, deep yellow; pistils yellow-green, erect or divergent, but not widely spreading, 4-7 mm. long, with slender styles, 1.2-3 mm. long; seeds pyriform, reddish-brown, 1 mm. long.

This is at once the commonest and most widely distributed species of the subgenus *Gormania*. It may be recognized by its creeping habit, its abundant rosettes of loosely arranged fleshy leaves and the three-parted cymes of yellow flowers with the petals distinct to the base.

Three subspecies may be distinguished. These differ primarily in vegetative characteristics. All have been transplanted from the wild to Ithaca, New York, where they have been grown under uniform conditions. Since they continue to maintain their distinctive characteristics after three years of culture, they seem

1. Sedum spathulifolium

. Seaum spathulifolium

to be really different genetically, and not physiological variants. This conclusion is further supported by the fact that the three subspecies have different cultural requirements if one wishes to maintain each in optimum condition. The vegetative differences between the subspecies of S. spathulifolium and S. Purdyi are shown in plate 22, fig. 3.

KEY TO THE SUBSPECIES OF SEDUM SPATHULIFOLIUM

A. Leaves of rosettes 2-3 mm. thick, very pruinose; rosettes 1.0-6.0 cm. in diam.; stems of offsets 1.5-3 mm. thick, frequently leafy throughout, but with a rosette-like cluster of leaves at the apex	1b. S. spathulifolium subsp. pruinosum
AA. Leaves of rosettes green or glaucous, not de-	
cidedly pruinose, 1-2 mm. thick; rosettes 1-5	
cm. in diam.; stems of offsets 1-2 mm. thick	
with the leaves usually restricted to the	
rosettes which are terminal on the shoots	В
B. Leaves glaucous, crenulate; stems of offsets	
1.5-2 mm. in diam.; flowers 8-17 mm.	* ~ ~ ~ ~ ~ ~
in diam.	1a. S. spathulifolium subsp. typicum
BB. Leaves green, usually neither glaucous nor	
pruinose, minutely crenulate; stems of	
offsets 1–1.5 mm. in diam.; flowers 7–11	
mm. in diam.	1c. S. spathulifolium subsp. anomalum

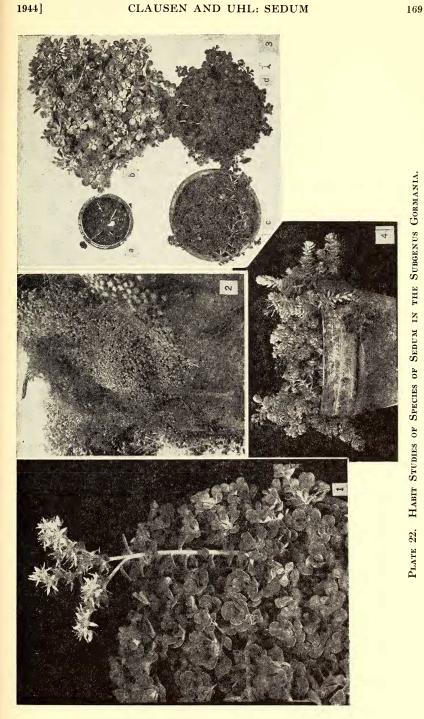
1a. SEDUM SPATHULIFOLIUM Hooker subsp. typicum. Sedum spathulifolium Hooker, Flor. Bor. Am. 1: 227. 1834. S. californicum Britton, Bull. N. Y. Bot. Gard. 3: 44. 1903. S. Woodii Britton, No. Am. Flora 22: 73. 1905.

The distinctive features of subsp. typicum are the glaucous leaves, the more slender habit compared with subsp. pruinosum, and the slightly larger size compared with subsp. anomalum. These vegetative differences are well demonstrated by figure 3 (pl. 22). In floral characters, the subsp. typicum is likewise intermediate between the other two subspecies. The three-parted cymes usually contain from 20-40 flowers which are 8-17 mm. in diameter.

PLATE 22. HABIT STUDIES OF SPECIES OF SEDUM IN THE SUBGENUS GORMANIA. FIG. 1. Sedum spathulifolium subsp. typicum, cultivated in greenhouse at Ithaca; collected along Grave Creek, Josephine County, Oregon. Photo by W. R. Fisher. FIG. 2. Sedum spathulifolium subsp. pruinosum, on rocks along Pacific Ocean, south of Crescent City, California. Photo by Harold Trapido. FIG. 3. Rosettes cultivated in greenhouse at Ithaca: a, Sedum Purdyi, from canyon of Canyon Creek, Siskiyou County, California; b, Sedum spathulifolium subsp. pruinosum, from rocks along Pacific Ocean south of Crescent City, Cali fornia; c, Sedum spathulifolium subsp. anomalum, from Yosemite National Park, California; d, Sedum spathulifolium subsp. typicum, from Josephine County, Oregon. Photo by W. R. Fisher. FIG. 4. Type collection of Sedum spathulifolium subsp. pruinosum var. "Cape Blanco," cultivated at Ithaca. Photo by W. R. Fisher.

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EXPLANATION OF THE FIGURES. PLATE 22.



The subsp. *typicum* is widely distributed in the northern Coast Ranges, the Cascade Mountains and the northern part of the Sierra Nevada. It occurs from the lower Bella Coola and Fraser

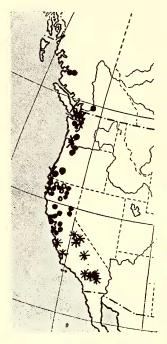


FIG. 2. Map showing distribution of the species and subspecies of the section Rosulata of Sedum: $\bullet = S$. spathulifolium subsp. typicum; $\times = S$. s. subsp. pruinosum; * = S. s. subsp. anomalum; $\bigcirc = S$. Purdyi. River valleys in British Columbia, to the Santa Cruz Peninsula in California. The altitudinal range is from 92 to 1920 meters. Since most of the specimens examined are without information about altitude, it is likely that this range will be increased as more data become available. The subsp. *typicum* usually grows in rocky places in ravines and canyons and on steep slopes.

Specimens seen. Highest altitude: 1920 m., 3 km. east of White Mt., Siskiyou Mts., Siskiyou Co., Calif., Wheeler 3171 (NY); lowest altitude: 92 m., 3 km. south of Oregon City, Clackamas Co., Ore., Clausen and Trapido 4925 (CU); northernmost: 52°30' N., Burnt Ridge Creek, 50 km. east of Bella Coola, Skeena Co., B. C., McCabe 1510 (UC) (Since the dried specimens are poor, their identity is questionable. This occurrence should be checked by further collections); easternmost: 120° W., Emigrant Gap, Calif., Jones 3345 (CLOK, NY); westernmost: 124° W., Snow Camp Lookout, Curry Co., Ore., Leach 2292 (ORE); southernmost: 37°30' N., Los Gatos Cañon near Los Gatos, Santa Clara Co., Calif., Heller 7422 (FM, UC); oldest: Sept. 25, 1861, summit of Mt. Diablo, Calif., Brewer 842 (UC); type: not seen (collected by

Douglas on dry rocks of the Columbia and Salmon rivers); types of names assigned to synonymy: north side of Mount Shasta, Siskiyou Co., California, alt. 5000–9000 ft., June 11–16, 1897, Brown 336 (type of S. californicum Britton, NY); Oregon City, Oregon, 1866, Wood (type of S. Woodii Britton, NY). Number of collections seen: 63. Specimens of this subspecies examined in connection with the present study have been annotated as Sedum spathulifolium Hooker, subspecies A.

Hooker described *Sedum spathulifolium* as common on dry rocks of the Columbia and Salmon rivers. His description is not sufficiently complete to make positively certain which of the subspecies he was describing. Our basis for interpretation of the name rests on the plants which are the prevalent kind in the valley of the Columbia River. We have seen no specimens from

as far inland as the Salmon River. The type specimen of S. californicum looks like typical S. spathulifolium, but the leaves are pruinose in the dried condition and Britton described the petals Possibly the color of the flowers may have faded, as as white. sometimes happens. Cooke, in a letter of January 13, 1941, and in a publication (6), questioned whether the specimens of S. californicum and other of Brown's collections really originated on Mt. Shasta. He favored the idea that they came from the eastern ridges or ranges of the Klamath Province. According to Cooke, A. A. Heller who knew Brown personally, wrote that no doubt all of Brown's Sedum collections were made somewhere on Mt. Eddy. As far as we understand the present distribution of these plants, this theory impresses us as reasonable, particularly since Cooke has been unable to find the plant on the north side of Mt. Shasta, and Trapido and the senior writer were likewise unsuccessful in their search there in 1940. At Oregon City, the type locality of S. Woodii, Trapido and the senior writer found S. spathulifolium frequent on rocks, but plants from there do not seem distinctive.

The time of flowering and fruiting depends somewhat on the latitude and on the altitude. Extreme dates of flowering for three districts, as determined from data with herbarium specimens, are:

> Santa Cruz Peninsula, Calif. ... April 28-May 28 Western Oregon May 9-June 24 Fraser River Valley, B. C. June 15-July 15

A dwarf variety, collected originally at 1524 meters, at Snow Camp Lookout in Curry Co., Ore., has been designated by Henderson (in M. E. Peck, Man. High. Plants Oregon. p. 360. 1941) as var. minus. This may interest horticulturists and should be listed as a variety under subsp. typicum. The type is in the herbarium of the University of Oregon. Praeger's var. purpureum should be referred to subsp. pruinosum and his var. majus to subsp. anomalum, though both these varieties have in the past been placed under typical S. spathulifolium.

Plants of six collections have been studied cytologically. All are n = 15. Previously, Hollingshead (9) had reported a diploid number of 30 for three of the collections of *S. spathulifolium*. Collections for which the euploid number is now reported are: *Clausen* and *Trapido 4925*, South Fork of Eel River, 8 km. west of Hullville, Lake Co., Calif.; *Clausen* and *Trapido 5010*, north side of Grave Creek, 1.4 km. east of junction with Rogue River, Josephine Co., Ore.; *Clausen* and *Trapido 5022*, bluffs along east side of Willamette River, 3 km. south of Oregon City, Clackamas Co., Ore.; and *Clausen 77, 141* and 324, all from cultivated sources. The chromosome complements of these several collections are sufficiently similar that one collection cannot be separated from another on a basis of the chromosomes. There is some variation

in the size of the chromosomes in a complement, but none of the chromosomes are sufficiently distinctive to be identified.

Sedum spathulifolium subsp. typicum is frequent in the horticultural trade. It is grown in rock gardens and is usually correctly named as to species. Rarely it is listed as S. Woodii. The var. minus also is offered. Other varieties are listed, but these are either referable to other subspecies or are nomina nuda.

The first illustration of typical S. spathulifolium seems to have been published in 1883 in the Garden (vol. 24, page 462). An earlier plate which appeared in Gartenflora in 1872 is so poor that there is doubt whether the plant figured really is S. spathulifolium.

1b. SEDUM SPATHULIFOLIUM Hooker subsp. pruinosum (Britton) Clausen et Uhl, comb. nov. Sedum pruinosum Britton, No. Am. Flora 22: 72. 1905.

The distinctive characteristics of subsp. pruinosum are the very pruinose condition of the leaves, stems, floral bracts and calyx; the large size, with the leaves of the rosettes 2-3 mm. thick; and the stout sterile stems, 1.5-3 mm. thick, which are frequently leafy throughout, whereas in the other two subspecies the leaves usually occur only in dense rosettes at the ends of the shoots. In cultivation at Ithaca, subsp. pruinosum maintains its distinctive characteristics and thrives more successfully than do either of the other two subspecies. Also it seems to prefer more moisture. Whereas subsp. anomalum scarcely persists under the same conditions of culture, subsp. pruinosum becomes robust, flowers and spreads.

The subsp. pruinosum is restricted almost entirely to rocks and bluffs along the Pacific Ocean from near Little River, Humboldt County, California, to Nanaimo on Vancouver Island. In the "Preliminary Catalogue of the Flora of Vancouver and Queen Charlotte Islands" (10), the report of Sedum spathulifolium from the Queen Charlotte Islands may refer to subsp. pruinosum, but we have not seen specimens from there. The altitudinal range is not great, essentially from sea-level to about 30 meters or perhaps a little higher. The plants trail, creep or even hang over the boulders along the coast, often forming great patches or mats on the rocks. They must frequently be bathed in the spray of the surf. Two collections from along the lower course of the Columbia River and several from the islands of Puget Sound suggest that this population is connected with the population of subsp. typicum of inland districts by specimens somewhat intermediate in character and should not be segregated as a separate species. This opinion must yet be checked by genetical experiments.

Specimens seen. Highest altitude: 30 m., coast bluffs near Trinidad, Humboldt Co., Calif., *Tracy 2582* (UC); lowest altitude: 3 m., 8 km. south of Crescent City, Del Norte Co., Calif., *Clausen* and *Trapido 4937* (BH, CU, NY, US); northernmost: 49°10' N., Nanaimo, *Rosendahl 1886* (CLOK); easternmost: 122°30' W., Lummi Island, Whatcom Co., Wash., Muenscher 7930 (CU); westernmost: 124°10' W., Gold Beach, Curry Co., Ore., Hoyt 64 (DS); southernmost: 41°2' N., south of Little River, Humboldt Co., Calif., Wiggins 5878 (FM, UC); oldest: 1887, Cedar Hill, Vancouver Island, B. C., Macoun (NY); type: Crescent City, California, 1903, Eastwood (NY). Number of collections seen: 32. Specimens of this subspecies, examined in connection with the present study, have been annotated as Sedum spathulifolium Hooker, subspecies B.

Miss Eastwood sent Dr. Britton a fresh piece of her original collection. This was cultivated in New York and flowered there on May 8, 1904 (N. Y. Bot. Gard. no. 18748, Rose 540). The type appears pruinose and consists of two floral stems, plus a few leaves. There are really no good rosettes on the specimen. Living plants and herbarium specimens collected by Trapido and the senior writer on cliffs and ledges along the shore of the Pacific Ocean 8 km. south of Crescent City, on July 24, 1940 (Clausen and Trapido 4937) are good matches for the type of S. pruinosum and have been our basis for interpretation of the name.

Extreme dates of flowering are April 27 and July 24. The flowering period is more prolonged than in subsp. *typicum*, also it is earlier at any given latitude. Undoubtedly this feature may be explained, at least partly, on a basis of the lower altitude at which subsp. *pruinosum* occurs and the consequent milder climate.

Principal variations are in the color of the leaves and stems and in size. Praeger (12, p. 239) has described a var. *purpureum* with the leaves purple. We have grown this in Ithaca, having obtained specimens from two different horticultural sources. The plants are definitely referable to subsp. *pruinosum*, under which the variety should be listed. At least two other unpublished varietal names, likewise referable to subsp. *pruinosum*, are also in the trade.

Plants of two collections have been studied cytologically: W. C. Muenscher 7930 from Lummi Island, Washington; and Clausen and Trapido 4937 from Crescent City, California. Both collections are n = 15. Previously, Hollingshead (9) had reported 2n = 30 in root-tips of the Muenscher collection (7930).

The subsp. pruinosum is probably as common in the horticultural trade as subsp. typicum, but it is usually offered as S. spathulifolium. Rarely it is listed as S. pruinosum. The var. purpureum is available under that or other varietal names indicating reddish foliage. This subspecies is definitely to be recommended for culture by eastern gardeners. Particularly desirable are plants of the type which probably originated at Cape Blanco in Oregon. We now name this as Sedum spathulifolium subsp. pruinosum var. "Cape Blanco" var. nov. Hort., with the rosettes 1-2 cm. in diam., usually densely crowded, and with the leaves small, convex dorsally and ascending. As type we designate the specimen (S 266), cultivated at Cornell University, Ithaca, which is shown in figure 4 (pl. 22).

Figure 2 (pl. 22) shows the habit of the plant in nature. A drawing of a flowering plant, probably to be identified as this subspecies, appeared in Gardeners Chronicle in 1876 (vol. 5, p. 821).

1c. SEDUM SPATHULIFOLIUM Hooker subsp. anomalum (Britton) Clausen et Uhl, comb. nov. Gormania anomala Britton, Bull. N. Y. Bot. Gard. 3: 30. 1903. Sedum yosemitense Britton, ibid., p. 44. S. anomalum (Britton) Britton, No. Am. Flora 22: 72. 1905.

The most distinctive characteristic of Sedum spathulifolium subsp. anomalum, when seen in the field, is the non-glaucous condition of the leaves. This feature is likewise exhibited by cultivated specimens, whereas plants of the other two subspecies, when grown side by side with subsp. anomalum, under the same circumstances, exhibit the glaucous or pruinose condition. Another feature of subsp. anomalum is the usually smaller size, with the rosettes rarely more than 2.5 cm. in diameter. For the most part, the stems of the offsets are rather slender, 1-1.5 mm. in diameter.

The subsp. anomalum, found only in California, ranges along the west slope of the Sierra Nevada, from the region of Yosemite National Park southward to the San Bernardino and San Gabriel mountains. Along the coast it extends as far north as the headwaters of the Carmel River. It has been collected most frequently in the Sierra Nevada and the San Bernardino and San Gabriel mountains. The altitudinal range is from a little above sea-level to 2286 meters. The usual habitats are rocky slopes and hillsides, ravines and ledges.

Specimens seen. Highest altitude: 2286 meters, CALIFORNIA. San Bernardino Mts., Crawford 911 (POM); lowest altitude: 30 m. ± ?, Gragg's Canyon, San Luis Obispo Co., Moran 421 (BH); northernmost: 37°50' N., Hetch Hetchy Valley, Yosemite National Park, Hall and Babcock 3380 (UC); easternmost: 117° W., Bear Creek, San Bernardino Mts., Pierce (UC); westernmost: 121°30', Pine Valley, head of Carmel River, Goldman 762 (FM); southernmost: 34°2' N., pipe line trail on Yucaipa Mts., Reed 2769 (UC); oldest: 1865, Yosemite Valley and Mts., Torrey (NY); type: sandy hills in the path of strong daily sea winds, San Luis Obispo Co., June, 1883, Summers (NY); type of Sedum yosemitense Britton (NY), assigned to synonymy: Yosemite Valley between Vernal and Nevada Falls, 1677 m., July, 1902, Hall and Babcock 3425.Number of collections seen: 33. Specimens of this subspecies, examined in connection with the present study, have been annotated as Sedum spathulifolium Hooker, subspecies C.

A collection from the San Bernardino Mountains (*Clausen* and *Trapido* 4748), is a reasonable match for the type of Britton's

Gormania anomala and has been used by us as a standard in our comparison of living plants. A specimen from the type locality of S. yosemitense, in Yosemite Valley below Nevada Falls (Clausen and Trapido 4802), is a good match for the type of that species. Plants of the collections cited above (4802 and 4748), when grown under uniform conditions at Ithaca, became very similar and had the same cultural requirements. There seemed to be no real differences between these plants.

May and June are the principal months of flowering. Extreme dates when flowering specimens have been collected are April 30 and July 4, with one record of it being found in flower in the San Bernardino Mountains in November.

Two varieties of subsp. anomalum occur, one with white flowers and the other with the whole plant larger in size. The latter has been named var. majus by Praeger (12, p. 238). Our basis for referring it to subsp. anomalum rests on the fact that the leaves are green, not glaucous. Large specimens, similar to what Praeger has described, have been seen in the Santa Barbara Botanic Garden. These came originally from San Luis Obispo County and were collected by Reid V. Moran. This is the region of the type locality, but other plants from there were not nearly so large. It is possible that variety majus is only a physiological form, a response to richer soils, shade and increased moisture. If further collections from San Luis Obispo County should reveal that most of the plants from there are large and perhaps slightly glaucous, then Gormania anomala may need to be referred to subsp. typicum and the name yosemitense used for the subspecies of the Sierra Nevada and the San Bernardino and San Gabriel mountains.

Two collections, studied cytologically, are n = 15. These are from Cascade Canyon, San Gabriel Mountains, California (*Clausen* and *Trapido* 4748), and from below Nevada Falls, Yosemite Valley, California (*Clausen* and *Trapido* 4802).

Subspecies anomalum is rare in the horticultural trade. Judging from experience in growing it at Ithaca, it is difficult to maintain and less desirable than either of the other two subspecies.

Praeger's (12) illustration of S. yosemitense shows fairly well the aspect of subsp. anomalum.

2. SEDUM PURDYI Jepson, Fl. Calif. 2: 110. 1936.

Perennial with the stems procumbent or creeping, bearing flat rosettes of spatulate leaves; stems 1-4 mm. in diameter, 4-7 cm. long, light green to brown; leaves of rosettes closely imbricated with their apices pressed close together, spatulate or orbicularspatulate, rounded or truncate at apex, papillose on margins, 0.1-1.8 cm. long, 1-10 mm. wide, 1 mm. thick, yellow-green, granulose ventrally, waxy dorsally, sometimes lustrous; primary stems with offsets below rosettes, these radiating like the spokes of a wheel and naked except for the rosettes at their apices, 1.5-7cm. long, green; floral stems erect or slightly decumbent, 0-16

cm. high, 2-3 mm. thick below the inflorescence, with the leaves alternate, oblong-spatulate, spreading, 0.3-1.5 cm. long, 1-4 mm. wide; inflorescence a three-parted cyme of 10 to 39 flowers, with a central flower; floral bracts oblong-spatulate to linear, 2.5-5 mm. long; flowers sessile or short-stalked on pedicels to 2 mm. long, usually 5-merous, 1.5 cm. in diameter; sepals linear-lanceolate, obtuse or subacute, green, 2-2.5 mm. long; petals lanceolate, acute, 5-7 mm. long, spreading above the base, bright yellow to white; stamens 4 mm. long, anthers yellow or white; nectar scales 0.8 mm. long, 0.5 mm. wide, transversely oblong; pistils erect or divergent, gibbous ventrally, 4-7 mm. long, with the styles 1-2 mm. long; seeds pyriform, yellowish-brown, 0.8 mm. long.

The present known range of *Sedum Purdyi* is in the southern portion of the Klamath Mountains in northern California. We have seen specimens from altitudes of 183 to 617 meters, but Jepson mentioned the upper limit of altitudinal range as 4000 feet (1219 meters). The usual habitats are ledges and rocky slopes in shaded situations.

Specimens seen. CALIFORNIA. Highest altitude: 617 meters, east side of corral of Canyon Creek Camp, 1.6 km. up Canyon Creek from Scott River, 19 km. south of Hamburg, Siskiyou Co., *Clausen* and *Trapido 4983* (CU); lowest altitude: 183 meters, Somes Bar, Siskiyou Co., *Tracy 16271* (UC); northernmost: $41^{\circ}36'$ N., same as highest altitude; easternmost: $122^{\circ}40'$ W., near French Gulch, Shasta Co., *Rose* (CAS) (Jepson has cited the easternmost locality as Kennett, but we have seen no specimens from there); westernmost: $123^{\circ}30'$ W., same as lowest altitude; southernmost: $40^{\circ}42'$ N., same as easternmost; oldest: Aug. 21, 1908, Etna Creek, Siskiyou Co., *Butler 498* (CAS, UC); type: not seen (Etna Mills, Calif., Carl Purdy). Number of collections seen: 7.

A collection from ridges along Canyon Creek, Siskiyou County, California (*Clausen* and *Trapido 4983*) agrees for the most part with characters given in the original description of *S. Purdyi* and matches specimens from Mr. Purdy's nursery. This collection has been our basis for interpretation of the species. The rosettes are flat with the leaves closely compressed; the margins of the leaves are prominently papillose; and the petals are yellow, not white as stated in the original description. For directions to the locality at Canyon Creek, the senior writer wishes to express his gratitude to Mr. J. T. Howell of the California Academy of Sciences.

The flowering time is late in April. Flowering dates obtained from herbarium specimens are April 23 and April 29. Fruiting specimens with ripe seeds have been collected in late July. Plants obtained in flower in the Marble Mountains in August were probably blooming abnormally, since the usual time seems to be in the spring. No noteworthy variations of Sedum Purdyi have come to our attention. The species seems nearest to the subsp. anomalum of S. spathulifolium and, like that, is difficult to grow in the eastern part of the continent. Some specimens of the subsp. anomalum have appeared so similar to S. Purdyi that we have had difficulty in separating them, but usually the rosettes of S. Purdyi are more compressed and the margins of the leaves are more prominently papillose.

Plants of the collection from Canyon Creek Camp, cited above (*Clausen* and *Trapido* 4983), have been studied cytologically. These are n = 15.

Sedum Purdyi is occasionally offered in the horticultural trade and is usually correctly named.

Figure 3 (pl. 22) shows rosettes of the three subspecies of S. spathulifolium and of S. Purdyi. Note the slender stems of the secondary rosettes of the latter species.

SECTION EUGORMANIA CLAUSEN

Gormania Britton, Bull. N. Y. Bot. Gard. 3: 29. 1903. Named in honor of M. W. Gorman of Portland, Oregon. Type species: Cotyledon oregonensis Watson (Sedum oregonense).

A detailed discussion of this section has already appeared in print (3). For convenience, the key to species and the keys to the subspecies of *S. obtusatum* and *S. laxum*, with slight emendation, are repeated here. Otherwise, data are presented only when they are supplementary to the information in the earlier paper.

KEY TO THE SPECIES OF EUGORMANIA

	A.	Inflorescence and upper part of stem glandular	
		pubescent, strongly reflexed before flowering	
		time; leaves of rosettes glandular-ciliate; petals	
		yellow	6. Sedum Moranii
A	A.	Inflorescence and upper part of stem glabrous,	
		usually erect before flowering time; leaves of	
		rosettes usually not ciliate; petals yellow, white	
		or pink	В
		B. Flowers yellow or pale yellow, sometimes fading	
		to white or pink in age; inflorescence a	
		paniculate cyme; leaves of rosettes 1–3.5	
		cm. long	3. Sedum obtusatum
		BB. Flowers white, creamy white or pink; inflores-	
		cence a dense paniculate or corymbose	G
		cyme; leaves of rosettes 1–4.5 cm. long	C
		C. Flowers white or creamy white; sepals	
		ovate, 2–3 mm. long	4. Sedum oregonense
		CC. Flowers pink or pale pink, rarely white;	
		sepals lanceolate or ovate, 2–5 mm.	E Sadam Inner
		long	5. Seaum laxum

3. SEDUM OBTUSATUM A. Gray

Mr. Jack Whitehead has sent some large specimens collected originally by Mr. George B. Youngs from along the North Fork

of the Feather River, 4 km. north of Belden, Plumas County, California, and at an altitude of about 915 meters. These are characterized by very large rosette-leaves, up to 5 cm. long. The petals are pale yellow. These plants seem referable to S. obtusatum, but match neither subsp. typicum nor subsp. boreale. It is possible that they may represent an undescribed subspecies, since no material has previously been available from the Feather River region. One might expect that Sedum obtusatum from that section would be intermediate between the two described subspecies, but samples of the plants obtained by Mr. Youngs are larger than either of the other two races.

KEY TO THE SUBSPECIES OF SEDUM OBTUSATUM

A. Basal leaves relatively small, 0.5–2.5 cm. long, usu- ally broadly rounded or truncate at apex; stems	
of rosettes bright red	3a. S. obtusatum
	subsp. typicum
AA. Basal leaves usually larger, 1-3.5 cm. long, usually	
retuse at apex; stems of rosettes pale red or	
pink	3b. S. obtusatum
1	subsp. boreale
	22.5.pr oor oaro

3a. SEDUM OBTUSATUM A. Gray subsp. TYPICUM. No new data have accumulated regarding this subspecies.

3b. SEDUM OBTUSATUM A. Gray subsp. BOREALE Clausen.

A plant of the type collection (Clausen, Trapido and Cooke 4952) flowered in a greenhouse at Ithaca on May 7, 1943. The stamens were red and the carpels were suffused with red. The petals spread rather widely above the middle. The length of the basal leaves ranges up to 3.5 cm. long.

The senior writer wishes to express hearty thanks to W. B. Cooke for guiding him and Mr. Trapido to the locality on Mt. Shasta where subsp. boreale occurs.

4. SEDUM OREGONENSE (Watson) M. E. Peck.

The inflorescence is a paniculate cyme, not a true panicle. A plant, originally from Crater Lake, which flowered indoors at Ithaca, had yellow anthers.

5. SEDUM LAXUM (Britton) Berger.

Further study of living plants in cultivation necessitates a few changes in the key to the subspecies.

KEY TO THE SUBSPECIES OF SEDUM LAXUM

A. Plants tall and robust, 25-45 cm. high; leaves dark green to glaucous; stems of sterile rosettes pink, 4–6 cm. long; petals pale to 5b. S. laxum deep pink

subsp. typicum

- AA. Plants not as tall as above, 10–25 cm. high; leaves yellow-green or blue-green, usually glaucous; petals pink, pale pink to white suffused with pink
 - pink B. Inflorescence congested; rosettes closely crowded, forming a dense mat, with the leaves rather thin; stems of sterile rosettes green to black, 1.5-2 cm. long
 - BB. Inflorescence lax; rosettes not closely crowded, forming a loose mat, with the leaves thick and leathery
 - C. Rosette-leaves very broad, 2.0-3.0 cm. wide, triangular, obcordate, sometimes not glaucous; petals pale pink to white 5c. S. laxum
 - CC. Rosette-leaves narrow, 0.3-2.0 cm. wide, oblong-oblanceolate or spatulate, usually glaucous; petals pink
 D. Cauline leaves oblong-spatulate, longer than broad
 - DD. Cauline leaves cordate to subcordate, about as broad as long 5e. S. laxum

5d. S. laxum subsp. retusum

С

в

c. S. laxum subsp. latifolium

D

5a. S. laxum subsp. perplexum

> S. laxum subsp. Heckneri

5a. SEDUM LAXUM (Britton) Berger subsp. PERPLEXUM Clausen. No new data have come to hand.

5b. SEDUM LAXUM (Britton) Berger subsp. TYPICUM. Cultivated specimens originally from the type locality exhibit some variation in the glaucous condition of the leaves. Some rosettes are less glaucous than others. A collection of Clausen (5018) is n = 15. Previously, Dr. Hollingshead had reported a diploid number of 30 for this same collection. A cultivated plant, received as *Sedum Jepsoni*, is *Sedum laxum* subsp. *typicum*. That binomial was introduced into the literature by H. M. Butterfield (Desert Plant Life 8: 7. 1936).

5c. SEDUM LAXUM (Britton) Berger subsp. LATIFOLIUM Clausen. A specimen of the type collection, cultivated in a greenhouse at Ithaca, flowered in the spring of 1943. The inflorescence was 15 cm. long and 6 cm. wide. The stamens were 6-7 cm. long with the anthers red and the filaments white to pink. The pistils were 8 mm. long with the ovaries green and the styles and stigmas pink.

5d. SEDUM LAXUM (Britton) Berger subsp. RETUSUM (Rose) Clausen. Two additional years of culture of this subspecies have not affected its characteristic manner of growth. Cytological study of University of California no. 28.3 from Mendocino County, California, indicates that the haploid number is 15.

5e. SEDUM LAXUM (Britton) Berger subsp. HECKNERI (Peck) Clausen. No new data have become available regarding this subspecies.

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6. SEDUM MORANII Clausen. No new localities for this rare species have come to our attention.

SUMMARY

The subgenus Gormania of Sedum includes six species which together constitute a natural phylogenetic group restricted to the Pacific Mountain System of Western North America. Taxonomic, geographical and cytological data all confirm this opinion. The chromosome number, with one exception, is n = 15, 2n = 30. The exception is S. oregonense, of which the only plants so far studied are hexaploid. The species may be grouped in two sections, Rosulata and Eugormania, the former the more primitive. The section Oreganica, based on Sedum oreganum, does not belong in Gormania and should be referred elsewhere. The section Rosulata includes two species, S. spathulifolium and S. Purdyi. The section Eugormania includes the other four species: S. obtusatum, S. oregonense, S. laxum and S. Moranii. New botanical names are S. spathulifolium subsp. pruinosum and S. s. subsp. anomalum. A possibly undescribed subspecies of S. obtusatum is mentioned from the Feather River region in Plumas County, California.

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LITERATURE CITED

- 1. BERGER, ALWIN. Crassulaceae, in Engler and Prantl, Die Nat. Pflanzenfam. ed. 2. 18a: 352-485. 1930.
- 2. BRITTON, N. L. and J. N. Rose. Crassulaceae, in No. Am. Flora 22: 7-74. 1905.
- 3. CLAUSEN, R. T. Studies in the Crassulaceae-III. Sedum, subgenus Gormania, section Eugormania. Bull. Torrey Bot. Club 69: 27-40, figs. 1-3. 1942.
- and CHARLES UHL. The taxonomy of the subgenus Gormania of Sedum, in Abstracts of papers presented before the general, paleo-4. botanical, physiological, and systematic sections of the Botanical Society of America. Am. Jour. Bot. 29: 5s. 1942.
- and -Revision of Sedum Cockerellii and related 5. species. Brittonia 5: 33-46. 1943.
- 6. COOKE, W. B. First supplement to the flora of Mount Shasta. Am. Midl. Nat. 26: 74-84. 1941.
- FOSBERG, F. R. Subspecies and variety. Rhodora 44: 153-157. 1942.
 FRÖDERSTRÖM, HAROLD. The genus Sedum L. Act. Hort. Göt. 10 (4). App. 1-262, pl. 1-115. 1935. 9. HOLLINGSHEAD, LILLIAN. Chromosome studies in Sedum, subgenus Gor-
- mania, section Eugormania. Bull. Torrey Bot. Club 69: 41-43, figs. 1-5. 1942.
- 10. [KERMODE, F.] Preliminary catalogue of the flora of Vancouver and Queen Charlotte Islands. Prov. Mus. Nat. Hist., Victoria, B. C., pp. 1-87. 1921.
- 11. MAGOON, C. A. and ELMER SNYDER. Grapes for different regions. U. S. Dept. Agric., Farmers' Bull. 1936: 1-38. 1943.
- 12. PRAEGER, R. L. An account of the genus Sedum as found in cultivation. Jour. Roy. Hort. Soc. 46: 1-314, figs. 1-185. 1921.
- 13. WEATHERBY, C. A. Subspecies. Rhodora 44: 157-167. 1942.

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